

Passive Suspension Feeding by an Octocoral in Plankton Patches: Empirical Test of a Mathematical Model

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Abstract. Feeding rate in the octocoral, *Alcyonium siderium*, was investigated as a function of colony size, flow speed, and prey concentration. The feeding rate decreases with time in high prey concentrations. A model of passive suspension feeding is formulated that successfully predicts feeding behavior. At low prey concentrations, the model predicts a linear feeding response as particle flux or colony size increases. The dominant constraint on feeding is the "handling time" required to transfer prey from tentacle to pharynx and to re-extend the tentacle. The time constant of prey capture shows no relation to particle flux, in agreement with the model. Another constraint, the "filtration time," is inversely related to colony size and flow speed. Filtration time becomes important only during feeding in sparse prey concentrations, when feeding rate is proportional to flow speed, colony size, and prey concentration. In the field, *Alcyonium* colonies reduce filtration time by orienting at right angles to the dominant flow direction. Feeding efficiency on prey patches is low and inversely related to flow speed, colony size, and prey concentration. Feeding in patches is not a simple process for this octocoral, because colonies will "saturate" with prey before all polyps have successfully captured a single prey item.

Introduction

Suspension feeding occurs in nearly all animal groups (Jørgensen, 1966), and virtually every body of water possesses a guild of organisms making a living by filtering the soup in which they live. Groups that have received the greatest amount of attention in the literature are active suspension feeders, *i.e.*, those organisms that generate their

own feeding currents. Organisms that rely exclusively on environmentally produced currents to bring them food are termed passive suspension feeders.

Experimental studies on active suspension feeders led to the formulation of the first mathematical models of suspension feeding. Decreases in the concentration of particles in closed systems containing these animals could be easily monitored; use of a decreasing exponential model of filtration allowed calculation of pumping rate (Jørgensen, 1943). Coughlan (1969) reviews the use of the exponential model in calculating pumping rates (sometimes erroneously called filtration rates) for active suspension feeders. Filtration efficiency was assumed to be 100% in his treatment. Williams (1982) showed that if this assumption is seriously violated, the decline in cell concentration will be a double exponential, and measured declines cannot be easily converted into a filtration or pumping rate. His formulation of suspension feeding also predicts that the apparent filtration rate will be a function of time as physical limitations of the system with respect to filtration efficiency become important. Thus, apparent variations in filtration rate may be nothing more than manifestations of how sieving and other means of particle capture (Rubenstein and Koehl, 1977) interact with the population of cells of different sizes available for capture. Behavioral modifications of pumping rate need not be invoked to explain variation in pumping rate. Williams (1982) provides a prescription for measuring pumping rate accurately and testing for any behavioral modifications; this involves finding a particle that is filtered with 100% efficiency by the organism under investigation. Most active suspension feeders such as bivalves (Jørgensen, 1975; Mohlenberg and Riisgard, 1978; Palmer and Williams, 1980) and ascidians (Fiala-Medioni, 1973, 1978a, b, c, d) attain remarkable capture efficiencies for the small

particles on which they feed (bacterio- and phytoplankton). Efficiencies can often reach 100% for particles on the order of $10\ \mu\text{m}$ in diameter, and thus pumping rates can be easily measured following the recommendations of Williams (1982).

Predictions of mathematical models

Mathematical models have also been used to clarify the control of suspension feeding. Two complementary and not entirely separable approaches have been: (1) to predict how an organism's feeding rate should relate to the density or quality of the food it encounters (Holling, 1965; Emlen, 1973; Doyle, 1979; Seale, 1982) and, (2) to see whether suspension feeding organisms maximize the rate of energy gain (Lehman, 1976; Lam and Frost, 1976).

Both Holling (1965; functional response type I) and Lehman (1976) predict that ingestion or filtering rate should show a linear dependence on prey availability or density up to some saturation value in organisms such as cnidarians, where encounter rate with the prey is determined by organism size and environment (in this case, flow speed). The saturation level is presumably set by the digestive physiology of the organism, *e.g.*, the "packed gut" assumption of Townsend and Hughes (1981). An implicit assumption is that all prey encountered, or at least some constant fraction of them, are retained by the organism (constant efficiency); symbolically, $\frac{dN}{dt} = K$, where N = number of prey caught, and K is a constant. K can be further decomposed: $K = U \times V \times SA$, where U = flow speed, V = prey concentration, and SA is the surface area of the organism available for prey capture. I term this hypothesis the "linear" model of passive suspension feeding, which is typically used in analyzing passive suspension feeding.

The "linear" model predicts that for a given prey density below the saturation level, feeding rate should be constant. Figure 1A gives the solution to the linear model and shows how doubling the prey concentration, flow speed, or projected surface area (size) of the organism should affect the feeding "response." Note that this "filling" curve gives the cumulative number of prey caught as a function of time; it assumes that prey density is not changing as the organisms feeds. The "filling" curve is mathematically isomorphic with the functional response type I of Holling (1965) at a given prey concentration. The curve is also conceptually equivalent to viewing filtration as a Poisson process, *i.e.*, the probability (P) of capture during a small increment of time (Δt) is constant, and the magnitude of P is the product of U , V , and SA (Fig. 1B). Furthermore, the interval between capture events is large at low prey concentrations, for reasons to be discussed below, and hence capture events are rare.

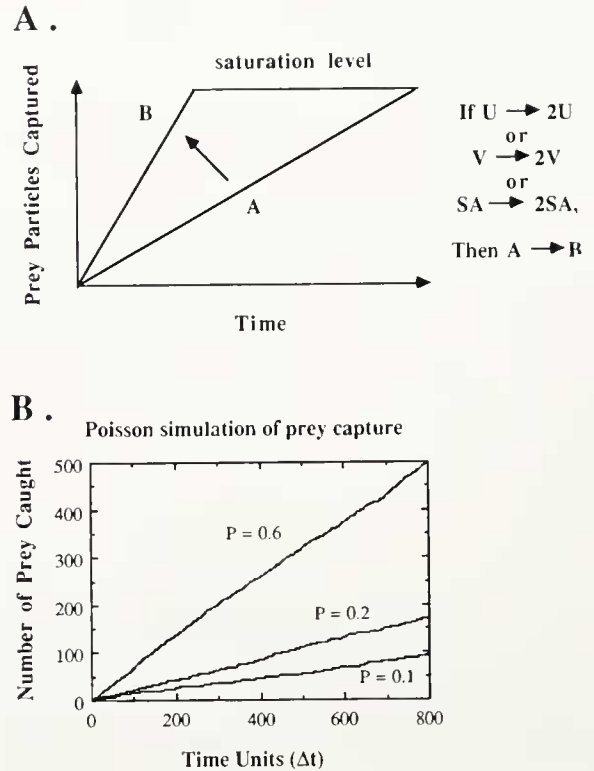


Figure 1. The classical view of passive suspension feeding. (A) The "linear" deterministic model of passive suspension feeding, which assumes prey encounter rate is proportional to the projected surface area normal to the flow (SA), the flow speed (U), and concentration of prey present (V). The feeding rate is constant until some saturating level of prey inside the organism is attained. This curve is implicit in Holling's (1965) type I functional response curve for predator-prey systems similar to passive suspension feeding. (B) The previous model is functionally equivalent to a process governed by the Poisson interval distribution, *i.e.*, a process where the probability (P) of capture during a small interval of time (Δt) is constant. The filling curves were generated by computer simulation for three levels of P , corresponding to increasing levels of flow, colony size, or particle concentration. Note the linear dependence between the number of particles captured and the time the suspension feeder has been exposed to a current carrying prey items.

Energy maximization arguments (*cf.* Townsend and Hughes, 1981) argue that filter feeders should feed preferentially on particles with the higher nutritional value, unless the cost of sorting and rejection are too high. The few tests in the literature (Doyle, 1979, amphipod; Seale, 1982, anuran tadpole larvae) indicate that these suspension feeders do behave in a manner consistent with energy maximization. Some work has addressed whether models formulated for other organisms make predictions compatible with observations of feeding rate as a function of prey density for passive suspension feeding in cnidarians (Clayton and Lasker, 1982). Sebens (1979, 1984) formulated a cost/benefit model for cnidarians using energy maximization as a means of predicting optimum organism size in a given habitat. The model has had good success

in predicting maximum organism sizes observed in the field. However, little attention has been paid to modeling the response of passive suspension feeders to dense prey concentrations, which may change suddenly in time, *i.e.*, what happens when a plankton patch sweeps by a cnidarian colony?

A dynamic mathematical model of passive suspension feeding

The limitations of the "linear" model are those imposed by its assumptions. Feeding rates may not be constant over time, especially if the handling of individual particles, or digestive or neurally mediated behavior becomes important. A more robust model of suspension feeding for cnidarian colonies was formulated and tested against real feeding in "patch" concentrations in the laboratory. The model takes a systems analysis view of passive suspension feeding; the input to the system (colony) is prey in the water column, the output is prey inside the organism. The model allows sudden changes in prey concentration and predicts the time course of feeding using two parameters. Congruence between the observed and predicted parameters of the model implies the assumptions used in the formulation are not too far from reality, *i.e.*, identification has been made of the salient features of the filtration system that determine feeding performance.

There are three model assumptions. (1) The colony "fills" up with prey at a rate proportional to the difference between the ambient plankton concentration (V_i) and the amount of prey already in the colony (V_o); symbolically, $(V_i - V_o)$. (2) The colony fills at a rate inversely proportional to the time necessary to handle the particles caught during filtering (R_1) and the time needed to filter the water containing the particles (R_2); symbolically, $\frac{1}{(R_1 + R_2)}$. Operationally, R_1 is the time taken to transfer, from tentacle to polyp mouth, the particle caught from a unit volume of water and to re-extend the tentacle; R_2 is the inverse of the filtration rate, which depends on the projected area of the organism perpendicular to the flow, and the flow speed. (3) A sudden jump in the plankton concentration results in a jump in the number of particles caught. The size of the jump is directly proportional to the jump in the particle concentration, $\frac{dV_i}{dt}$, the colony volume (C), and the proportion of time spent filtering particles during feeding, $\frac{R_2}{(R_1 + R_2)}$; symbolically, $C \frac{dV_i}{dt} \frac{R_2}{(R_1 + R_2)}$.

The first and second assumptions address the steady-state behavior of the passive suspension feeder, while the third deals with the dynamic aspect of prey capture. Ex-

pressed as a differential equation, passive suspension feeding may obey:

$$C \frac{dV_o}{dt} = \frac{(V_i - V_o)}{(R_1 + R_2)} + C \frac{R_2}{(R_1 + R_2)} \frac{dV_i}{dt}, \quad (\text{Eq. 1})$$

where $C \frac{dV_o}{dt}$ is the time change in the total number of particles caught by the organism.

Dividing by the size of the colony yields:

$$\frac{dV_o}{dt} = \frac{(V_i - V_o)}{(R_1 + R_2)C} + \frac{R_2}{(R_1 + R_2)} \frac{dV_i}{dt}. \quad (\text{Eq. 2})$$

Eq. (2) can be rearranged algebraically to:

$$\tau \frac{dV_o}{dt} + V_o = \alpha \tau \frac{dV_i}{dt} + V_i, \quad (\text{Eq. 3})$$

where $\tau = (R_1 + R_2)C$, and $\alpha = \frac{R_2}{(R_1 + R_2)}$. τ is the time constant of colony "filling," while α is the measure of how many prey are caught as the edge of the patch sweeps by the colony.

The solution to Eq. (3) depends on the nature of the change in the plankton concentration in the water column or laboratory flume. An electrical circuit that mimics exactly the behavior of this mathematical feeding model is called a lag-lead network (Milsum, 1966) and is shown in Figure 2. Formulation of the resistive-capacitive analog is motivated by the observation that prey filtration and prey handling are discrete processes. They are modeled as "resistances" through which the "current" of prey must pass to fill the organism's "capacity" (the etymological root of capacitance). This circuit can be easily wired up with variable resistors, $R_{1,2}$ and variable capacitor, C , allowing exploration of the model's qualitative behavior. A change in plankton concentration would be simulated by

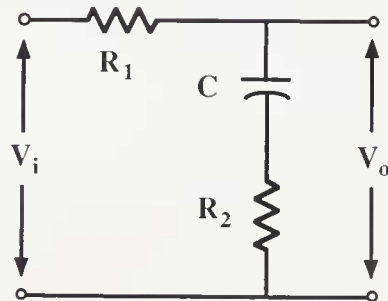


Figure 2. Electrical analog to the differential equations used to model the process of passive suspension feeding. The behavior of this circuit exactly mimics the model. R_1 is the handling time "resistance" and R_2 is the filtration time "resistance." The concentration of particles in the water column is a "voltage" (V_i) that may cause a "current" of particles to enter and reside inside the organism (V_o); this is controlled by the resistances, $R_{1,2}$ and the volume "capacitance" (C) of the animal.

a change in the input voltage (V_i); simulation of colony feeding response predicted by the model can be seen by watching the behavior of V_o as a function of time on an oscilloscope.

Applying Kirchoff's law to this circuit, I obtain:

$$iR_1 + \frac{1}{C} \int idt + iR_2 = V_i(t) \quad (\text{Eq. 4})$$

and

$$\frac{1}{C} \int idt + iR_2 = V_o(t), \quad (\text{Eq. 5})$$

where i is the "current" of particles.

Taking the Laplace transform of Eqs. (4) and (5) yields:

$$\left(R_1 + R_2 + \frac{1}{Cs}\right)i(s) = V_i(s) \quad (\text{Eq. 6})$$

and

$$\left(R_2 + \frac{1}{Cs}\right)i(s) = V_o(s), \quad (\text{Eq. 7})$$

where s is the frequency-domain variable. Some algebra then results in:

$$\frac{V_o(s)}{V_i(s)} = \frac{R_2 + \frac{1}{Cs}}{R_1 + R_2 + \frac{1}{Cs}} = \frac{a(s+b)}{b(s+a)} \quad (\text{Eq. 8})$$

where $a = \frac{1}{(R_1 + R_2)C}$, and $b = \frac{1}{R_2C}$.

Eq. (8) is the Laplace transform of Eq. (3). It can be rearranged to:

$$V_o(s) = s \frac{R_2C}{(\tau s + 1)} V_i(s) + \frac{V_i(s)}{(s + 1)} \quad (\text{Eq. 9})$$

To solve Eq. (9), the nature of the input change in plankton concentration must be specified. For a *step* increase in the plankton availability to level V_i , caused by a patch of plankton flowing past the colony, $V_i(s) = \frac{V_i}{s}$. Substituting, I obtain:

$$V_o(s) = s \frac{R_2C}{(\tau s + 1)} \frac{V_i}{s} + \frac{V_i(s)}{(\tau s + 1)}, \quad (\text{Eq. 10})$$

which can be rearranged to:

$$V_o(s) = s \frac{R_2C V_i}{(\tau s + 1)} + \frac{V_i}{s(\tau s + 1)}. \quad (\text{Eq. 11})$$

Taking the inverse Laplace transform, I obtain:

$$V_o(t) = V_i \{ 1 - (1 - \alpha)e^{(-t/\tau)} \}, \quad (\text{Eq. 12})$$

the solution in the time domain.

Since α and τ can be computed from known quantities, it is possible to compare predicted with observed values of these two model parameters. In particular, τ will be an important descriptor of how quickly a colony can use a change in plankton concentration. Figure 3A shows the "filling" curve for colonies of different size (C), while Figure 3B shows identically sized colonies as the ratio between "handling" time (R_1) and "filtration" time (R_2) changes. The implications of the behavior of this model, its decomposition into the "linear" model (Type I functional response) under certain conditions, and the extent of its congruence with reality will be more fully developed in the Discussion section.

I experimentally tested this model by measuring feeding rates for a colonial cnidarian in the laboratory. *Alcyonium siderium*, an octocoral, is a dominant zooplanktivore on subtidal hard rock substrates in New England (Sebens and Koehl, 1984; Sebens, 1986). Colonies assume a variety of shapes varying from fingers to globose forms to compressed ellipsoids (Patterson, 1980). In plankton-rich

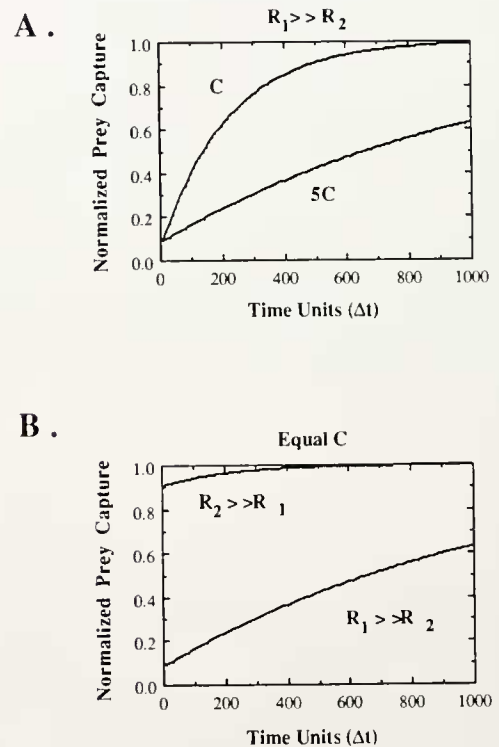


Figure 3. The time course of organism feeding as predicted by the model. (A) Colonies differing in size by a factor of five (C , $5C$) and with handling time (R_1) much greater than filtration time (R_2), as occurs during feeding in plankton patches. (B) Colonies of identical size where the handling time (R_1) is much greater than filtration time (R_2) and *vice versa*. The ordinates for both graphs are normalized for the effects of colony size. Note that if R_2 becomes much larger than R_1 , *i.e.*, the particle flux drops, then the filling curve tends toward a step function. Since particle flux is low, each passing particle is caught, and the model decomposes to the "linear" model of Figure 1.

habitats, fully expanded globose colonies can reach 10 cm in diameter. Previous work with *Alcyonium* colonies feeding in a closed system has shown that they readily accept prey particles (Patterson, 1984). This octocoral might be expected to follow the "linear" filling curve if prey concentration is held constant, and obey the changes predicted in Figure 1 as size and flow speed are varied. The aim of this laboratory feeding study was to test the "linear" model and the proposed alternative model for feeding in plankton patches. An intensive study of the diet of this species over a diel cycle (Sebens and Koehl, 1984) provides information useful in analyzing the results of this study.

Materials and Methods

Colony collection, maintenance, and flow generation and measurement

Feeding rate experiments were conducted at the Marine Science Center (MSC), Northeastern University, Nahant, Massachusetts, and in the biomechanics laboratory at the University of California, Davis. Colonies of *Alcyonium siderium* were collected by SCUBA diving and maintained in flowing seawater tables or recirculating chilled aquaria. Feeding observations were made in a recirculating flume described in Patterson (1984). All experiments were performed with the flow straighteners installed, which removed turbulence of length scales greater than 1 cm. Flow speeds and turbulence intensities were measured with a two channel thermistor flowmeter circuit modified from LaBarbera and Vogel (1976). The voltage output of the flowmeter was either connected to an eight-bit successive approximation A/D convertor (Mountain Computer) connected to an Apple IIe, or to a MacADIOS A/D convertor (GW Instruments) connected to an Apple Macintosh Plus. The sampling rate was 10 Hz.

Octocoral colonies attached to horse mussels (*Modiolus modiolus*) were collected subtidally from 15–23 m depth. Mussel shell fragments bearing *Alcyonium* colonies were mounted in the flow tank working section. The prey offered to the colonies were cysts of the brine shrimp, *Artemia salina*. Characteristics of the cysts are described in Patterson (1984). Capture of the cysts on individual tentacles of this species is readily observed. At the end of each feeding bout, three 60-ml samples were withdrawn isokinetically using a Cole-Parmer peristaltic pump (model no. 7568) smoothed with hydraulic capacitors. Samples were filtered onto gridded Millipore filters, the number of cysts was counted, and a mean concentration of particles present in the flow was calculated. The concentration of cysts offered (0.056–0.40 part./ml) was of the order of plankton concentrations seen in the field (Sebens and Koehl, 1984). However, even greater concentrations may be typical of dense patches of plankton that

are seasonally and spatially abundant (Fasham, 1978; Grosberg, 1982).

Documenting the time course of prey capture

Alcyonium colonies were introduced individually into the working section of the flume and allowed to acclimate to the flow. Prey were not introduced until the polyps were fully expanded. A standard volume concentration (0.45 g dry cysts/l) of *Artemia* cysts was added all at once to the flume. Observations of capture events were made at a magnification of 35X through a dissecting microscope suspended over the flume. A watch glass floating on the water and anchored over the colony prevented blurring of the image from capillary waves at the air/water interface. An interval timer program (0.05 s resolution) running on an Apple IIe microcomputer measured the time between capture events. The time required for a tentacle to transfer a captured particle to the pharynx ($\{R_1\}$ in the above model) was timed with a stop watch during separate experiments.

Filtration time for an individual particle was calculated using the projected surface area of the organism, and the flow speed measured 4 cm upstream of the top of the colony. Specimen volume was measured by volumetric displacement of water in a graduated cylinder. The number of prey caught as a function of time was plotted for each specimen; the observed values for the model parameters τ and α were obtained using a least squares algorithm, and then compared with the values predicted by the model calculations through linear regression.

Feeding efficiency

Efficiency of prey capture at the colony level was computed as follows: the number of particles caught by a colony during a standard feeding bout of 10 min was divided by the number of particles that would pass through the cross-sectional area occupied by the colony if the colony were not there. This is the standard engineering definition of efficiency of particle capture (Dorman, 1966). Because feeding rate at dense concentrations of prey is non-linear (Fig. 4), efficiency will be a function of time. Hence, for purposes of comparison, efficiency is computed over the time necessary to reach "saturation." Saturation is defined as the point at which capture events drop to less than one prey item caught per 5 min period *per colony*.

Field measurements of flow and orientation to flow

Field observations of orientation to flow in *Alcyonium* colonies and flow regime were made at the following sites (depths) in the subtidal of Massachusetts Bay: (1) Dive Beach site (8 m), located near Nahant, Massachusetts (42°25'N: 70°54'W), (2) Shag Rocks inner wall (7 m)

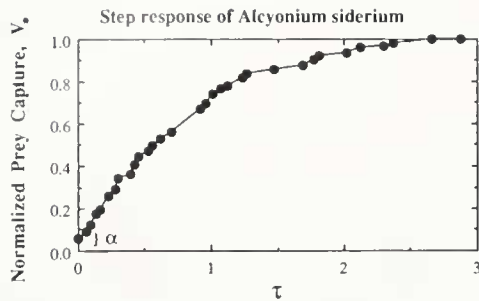


Figure 4. Typical feeding response of an *Alcyonium* colony to a step increase in the plankton concentration (*Artemia* cysts). The time axis (abscissa) is expressed in units of τ , a model parameter defined as the time necessary for the cumulative prey capture to reach $(1 - e^{-1}) = 63\%$ of the saturating value. The ordinate, V , is the cumulative number of prey captured normalized to the saturation level. Note that the response is curvilinear and can be characterized by two parameters, the time constant, τ , and α , the initial jump in plankton caught as the concentration changes.

located near Dive Beach, (3) Shag Rocks outer wall (9 m), and (4) Halfway Rock (14 m) ($42^{\circ}30'N$; $70^{\circ}46'W$). Orientation to the direction of current flow by colonies on subtidal rock walls was measured with a protractor and plumb line. The direction of current flow was determined with a filament of dye, and was parallel to the bottom and the wall. Flow measurements were made *in situ* at 1.0 cm and 10.0 cm height over *Alcyonium* colonies using a submersible thermistor flowmeter recording a digital signal on magnetic tape. Flow measurements were made over a three year period in all kinds of weather throughout the year. The sampling rate was 3 Hz.

Results

Feeding response to plankton patch concentrations

When *Alcyonium* colonies were subjected to sharp (step) increases in the plankton concentration, the "filling" curve was markedly curvilinear and showed an asymptote (see Fig. 4 for a typical example). Similar results were obtained with the sea anemone *Metridium senile* (unpub. data). At these high prey concentrations, doubling the flow speed and hence the particle flux typically had little effect on the feeding curve for a given colony (Fig. 5), providing evidence that the linear model of passive suspension feeding doesn't apply very well in patch concentrations.

Figure 4 gives the graphical interpretation of τ and α . Figure 6 shows how closely the model formulated in the Introduction predicts τ , the time constant, [time needed to reach $(1 - e^{-1})$ of saturation], and α , the proportion of prey caught as the edge of the patch sweeps past the colony at the start of feeding bout. Model I linear regression was used to test the ability of the predicted (calculated) model parameters to forecast the observed values. This type of

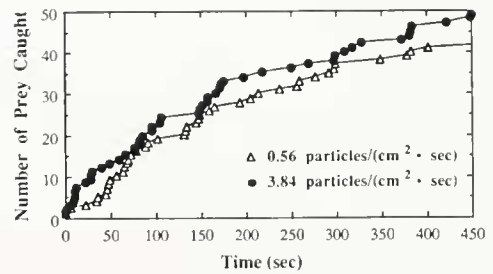


Figure 5. Feeding response of the same colony of *Alcyonium* to *Artemia* cysts offered at very different flux rates (flow speed $\{U\} \times$ particle concentration $\{V_i\}$). This effect is not predicted by the linear model (Fig. 1).

regression analysis is appropriate since the x values (the computed model parameters) were known precisely and fixed by the choice of colony (Sokal and Rohlf, 1981). Alpha values were log transformed before calculations of the regression to eliminate problems with non-normality. The aim of the model was to predict feeding behavior in dense suspensions to within a factor of two. The model achieves this goal in predicting τ and α . Linear regressions are $\tau_{\text{obs}} = 6.9 + 1.04 \ln(\tau_{\text{pred}})$ and $\ln \alpha_{\text{obs}} = -1.93 + 0.28 \ln(\alpha_{\text{pred}})$. R^2 values for these regressions for α and τ are 0.33 ($P = 0.05$) and 0.70 ($P = 0.0006$), respectively.

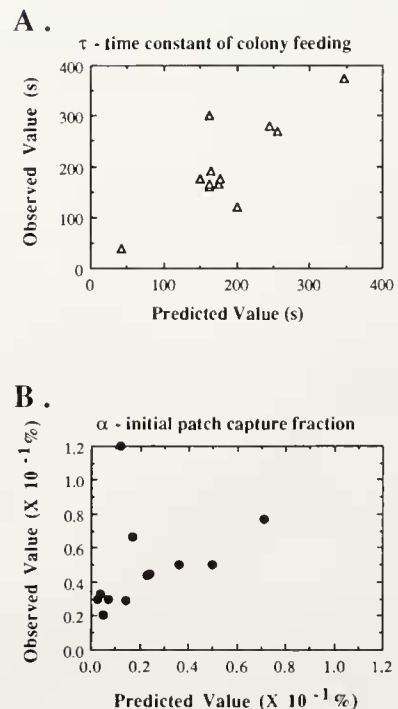


Figure 6. Predicted and observed values of (A) the time constant, τ , and (B) the patch edge capture fraction, α , for particle filtration by colonies of *Alcyonium siderium*. Predicted values of the model parameters were computed from the handling time (R_1), filtration time (R_2), and the colony volume (C).

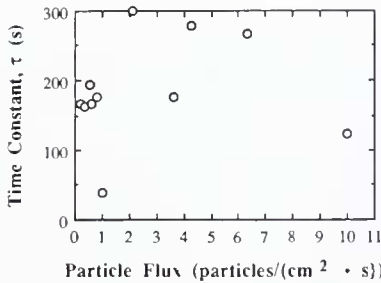


Figure 7. Plot of the time constant of colony filling, τ , as a function of the particle flux (flow speed $\{U\}$ X particle concentration $\{V_p\}$). The data do not have a slope significantly different from zero ($P < 0.001$) showing the lack of dependence of τ on particle flux at high flux rates.

Because $R_1 \gg R_2$ at the prey concentrations used, and $\tau = (R_1 + R_2) C$, R_2 will have little effect on τ . Thus a corollary to the model is that particle flux past the colony for high prey densities will have no correlation with the time constant (τ) or organism filling. This indeed was the case (Fig. 7). The model has slightly lower success in predicting the magnitude of α , which measures the degree to which a colony can "grab" the edge of a plankton patch as it sweeps by. Alpha is consistently overestimated; it is probably sensitive to colony shape and the precise patterns of flow obtained for a particular shape, and these aspects of passive suspension feeding were not part of the model formulation.

Colony size and feeding efficiency

Figure 9 demonstrates an inverse relationship between efficiency of capture (as defined in the Materials and Methods) and colony size. Smaller colonies are more efficient filters, although all sizes have very low efficiencies when feeding in dense concentrations. Figure 10 shows that there is also an inverse relationship between efficiency and flow speed, and hence particle flux, for a given particle concentration, for feeding by colonies.

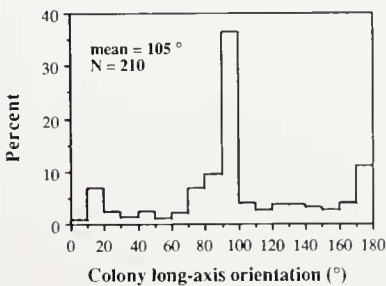


Figure 8. Orientation of the longest dimension of *Alcyonium* colonies to the local direction of current flow at four subtidal sites in Massachusetts Bay. Angles were measured with protractor and plumb line; current direction was determined with a filament of sodium fluorescein dye.

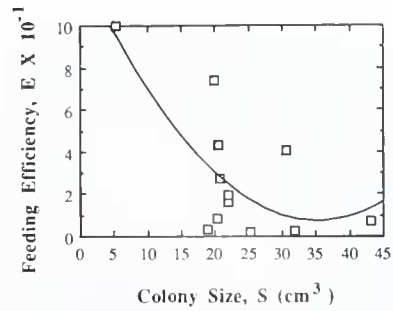


Figure 9. Efficiency of particle capture *per colony* (E) in *Alcyonium* as a function of colony size (S). Efficiency is defined as the number of particles caught by the colony in the time interval to saturation of the colony divided by the number of particles that would have passed through the space occupied by the colony. The regression is given by the equation: $E = 12.8 - 0.68S + (9.62 \times 10^{-3})S^2$ ($P < 0.05$; $R^2 = 0.55$; $df = 11$).

Discussion

The dynamics of cnidarian passive suspension feeding

Most cnidarians use passive suspension feeding, even though many forms such as scleractinian corals also possess symbiotic dinoflagellates that supply them with some large fraction of their nutrition (Muscatine and Porter, 1977). While the independence of zooplankton capture from autotrophy has been questioned (Clayton and Lasker, 1982), there is no doubt that for most boreal cnidarians lacking zooxanthellae, capture of particulate prey from the water column is of prime importance in their biology. Hence, modeling of the passive suspension feeding process is worthwhile because (1) it is ubiquitous in marine systems, (2) the particles filtered from the water column are patchy (Wiebe, 1970, 1971; Ortner *et al.*, 1984), *i.e.*, discontinuously distributed in space and time,

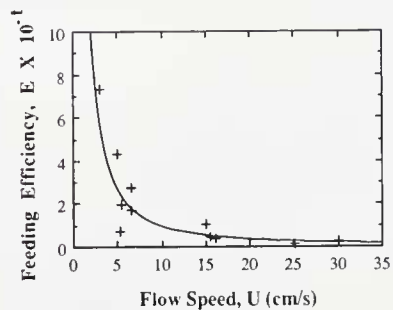


Figure 10. Efficiency (E) of particle capture *per colony* in *Alcyonium* as a function of flow speed (U). Efficiency is defined as the number of particles caught by the colony in the time interval to saturation of the colony divided by the number of particles that would have passed through the space occupied by the colony. The regression is given by the equation: $E = 32.30U^{-1.62}$ ($P < 0.05$; $R^2 = 0.81$; $df = 11$). These flow speeds correspond to a Reynolds number (Re) range of 800–12,000 calculated using the greatest dimension of each colony.

Table 1

Field measurements of flow speed 1.0 cm and 10.0 cm above colonies of *Alcyonium* at four subtidal sites in Massachusetts Bay (December 1981–September 1984)

Site	Depth (m)	1.0 cm			10.0 cm		
		Dives	Flow speed (cm/s)	Re $\times 10^2$	Dives	Flow speed (cm/s)	Re $\times 10^2$
Halfway Rock	14	10	18.8 (9.8)	90.8 (47.3)	11	18.4 (10.6)	88.9 (51.2)
Shag Rocks Inner	7	18	8.7 (7.2)	42.0 (34.8)	18	10.2 (9.7)	49.3 (46.9)
Shag Rocks Outer	9	20	10.5 (8.5)	50.7 (41.1)	21	11.3 (8.2)	54.6 (39.6)
Dive Beach	8	23	9.3 (7.1)	44.9 (34.3)	24	9.3 (7.6)	44.9 (36.7)

Flow was sampled at 3 Hz for 6 minutes per date.

Reynolds number (Re) was calculated for a colony 5 cm in greatest dimension.

Values are mean (standard deviation).

and the feeding response of these organisms to patches may have important effects on growth and metabolism (Szmant-Froelich and Pilson, 1984), or competition for food and space (Okamura, 1984), and (3) any predictive model must make assumptions that will offer insight into which features of the system are the most important.

Patchiness of particles is a common phenomenon in aquatic systems; the causes can be both biological (nutrient tracking, mass spawning) and abiotic (eddy entrainment) in origin (reviewed in Okubo, 1980). Passive suspension feeders respond to patchiness in interesting ways. Leversee (1976) found that an octocoral could alter its feeding rate in response to jumps in prey concentration. Crowell (1957) observed that a hydroid grew better on a single large daily ration of food than more frequent feedings, implicating more efficient digestion in a packed gut (coelenteron). Lasker *et al.* (1982) discovered that *Hydra* interrupts its feeding to digest its prey; therefore a single large feeding (dense prey) is just as good as a continuous supply. The response of *Alcyonium* to patch concentrations is interesting, especially when contrasted with the capture of prey in the field under more dilute conditions (Sebens and Koehl, 1984).

Lasker *et al.* (1982) used prey concentrations more than an order of magnitude greater than those used in this study. Plankton densities over coral reefs (Alldredge and King, 1977) and near boreal subtidal rock walls (K. Sebens, Northeastern University, pers. comm.) can often be greater than those in the water column nearby. Densities of plankton in freshwater aquatic systems are typically on the order of tens of plankters per liter (Wetzel, 1975); comparable densities are found in New England inshore waters (Sebens, 1984). The concentrations used in this study were on the order of 100/l. By comparison, oligotrophic oceanic waters usually have less than one zooplankter per liter (Ortner, *et al.*, 1981). Feeding on high densities of prey resulted in a curvilinear feeding response for the octocoral species investigated in this study. *Al-*

cyonium did not feed markedly faster at enhanced levels of prey density, in contrast to previous work with scleractinians (Lasker, 1976; Clayton and Lasker, 1982).

Handling time, filtration time, and flow in the field

Part of the error in the predictions of the parameter values of the model (Fig. 6) can be attributed to the variation in handling time (R_1). The mean handling time for a particle was 8.0 s (SD = 3.0; n = 20 colonies). It was not possible to measure handling time and capture events simultaneously, so the mean handling time was used to calculate the model parameters. The filtration resistance (R_2), is not subject to as wide a variation within a colony unless the organism changes its size by pumping water into its gastrovascular spaces. Size change is usually a response to severe hydromechanical stress (*cf.* Patterson, 1980); these organisms do not appear to regulate feeding rate through size changes except to turn feeding on and off. Robbins and Shick (1980) found similar behavior in the sea anemone *Metridium senile*. Colonies did not change size during the course of these feeding experiments. During ontogeny, the potential exists for *Alcyonium* colonies to reduce the value of the filtration time, R_2 , by growing in an oriented fashion to the predominant direction of flow. This indeed seems the case (Fig. 8).

The flow regime experienced by these colonies over a three year period at the four sites demonstrates a wide range of flow speeds (Table 1), with mean flows on the order of 10–20 cm/s. This corresponds to a whole colony Reynolds number of *ca.* 5,000 to 10,000. The flow at these depths is tidally driven and is often dominated by wave-induced oscillations (Patterson and Sebens, 1989). Colonies generally do not feed as velocities approach 50 cm/s (unpubl. obs.) and instead begin contraction.

The time constant of organism "filling" (τ) depends on colony size, handling time, and filtration time. Handling time was so much larger than filtration time for the particle

fluxes tested, that it dominated the time constant. For example, at the lowest particle flux tested $\{0.25 \text{ part./}(\text{cm}^2 \cdot \text{s})\}$, the handling time was three orders of magnitude greater than the filtration time for a typical colony with a projected surface area of 10 cm^2 . At what particle flux would the handling time and the filtration time become comparable in magnitude, *i.e.*, at what particle concentration and flow speed would passive suspension feeding be expected to be *responsive* to the *changes* in particle flux? For the same size colony considered above, the handling time will equal the filtration time at a particle flux of $0.01 \text{ part./}(\text{cm}^2 \cdot \text{s})$. What are particle fluxes like in the field?

Comparison with field data: do colonies become more efficient at lower particle fluxes?

Using the data of Sebens (1984) and Sebens and Koehl (1984), it is possible to calculate how many particles are caught by *Alcyonium* in the field, and make some order of magnitude calculations of the particle flux they are experiencing. Knowing the prey caught and the particle flux, we can calculate efficiency of capture. Particle flux is the product of prey concentration and flow speed. Flow speeds have been measured (Sebens, 1984; Table I) and Sebens (1984) reports plankton concentrations averaging about $3500 \text{ zooplankters/m}^3$, or 3.5 particles/l , in the warmer months of the year at the Nahant, Massachusetts, sites. Flow speeds are on the order of about $10\text{--}20 \text{ cm/s}$ measured 1.0 cm above the tops of *Alcyonium* colonies. The integrated flow over the colony will show a lower mean value, since the flow speed is reduced as one approaches the substrate through the logarithmic boundary layer (Denny, 1988).

Calculations show that a mean particle flux of $0.04 \text{ particles}/(\text{cm}^2 \cdot \text{s})$ occurs around these colonies in the field, not far from the value necessary for equality of the handling time and filtration time for *Alcyonium* [$0.01 \text{ particles}/(\text{cm}^2 \cdot \text{s})$]. If the mean flow speed is *ca.* 1 cm/s , the particle flux will be reduced another order of magnitude. Now the filtration time will be much greater than the handling time. Under such conditions, increases in the flow speed or prey concentration will cause an increase in the feeding rate, and a quasi-linear response will be found, similar to that predicted by the linear model! The model described in the Introduction decomposes to the "linear" model of passive suspension feeding described above when the particle flux past the organism is low. When R_2 (filtration time) is large compared to R_1 (handling time), α becomes almost one. The second term of Eq. (12) goes to zero; hence prey in the water becomes prey in the organism. In essence, as the particle flux becomes lower (through slower flow or lower prey concentrations), the model predicts instantaneous step responses

(capture) of single plankters or 100% efficiency. Are field data on feeding consistent with this prediction of high feeding efficiency?

Sebens and Koehl (1984) sampled gut contents of the sea anemone, *Metridium* and *Alcyonium* over a diel cycle. Using Sebens (1984), the plankton concentration for the site averages about 4 plankters/l during the warmer months. Assume the prey inside the organisms were caught during the previous two hours as *per* Sebens and Koehl (1984). Their data give a mean number of prey per colony of *Alcyonium* ($n = 90$). Assume each *Alcyonium* colony had a projected surface area normal to the flow capable of capturing prey of 10 cm^2 . Given the above plankton density, and an efficiency of 100%, a current of 2.1 cm/s would be needed to account for the gut contents. This flow speed is within the typical range of speeds seen above these organisms (Table I). Of course, these calculations are crude estimates because (1) different sizes and types of plankton are lumped in particle counts, and (2) both species prefer certain types of plankton over others. But high efficiencies for prey capture in *Alcyonium* seem reasonable for field values of flow and prey concentration (non-patch conditions).

Efficiencies measured under very high particle concentrations in the flume were an order of magnitude lower than these field estimates. *This dichotomy is predicted by the model*; at very high plankton concentrations, feeding becomes uncoupled from particle flux; under field conditions, efficiencies skyrocket, presumably due to the lower particle flux and hence favorable (R_2/R_1) ratio. Why couldn't these feeding experiments be repeated in the laboratory using particle fluxes representative of non-patch concentrations? In the flume, feeding was studied at high concentrations over short period of time for two reasons: (1) concentration and hence particle flux remained constant in the flume only over a period of 30 min; after that time, gravitational settlement significantly affects concentration, and (2) at realistic concentrations, capture events are on the order of minutes to large fractions of an hour apart, and would be tedious to document, even if concentration could be kept constant. Using SCUBA, I did spend several hours observing colonies of *Alcyonium* feeding *in situ* at the four sites sampled for flow speed. Because the particles on which they feed are only a few hundred micra in length, this requires approaching within 30 cm of the colony to observe capture events; this necessarily alters the flow around the colony. Only rarely in the field did I see "rapid" capture of prey at a rate comparable to that seen in the flume (seconds between captures); during these rare events there was an easily discerned "cloud" of copepods near the colonies. However, most of the time, the interval between prey capture events (visible particle adhesion followed by movement of the tentacle towards the pharynx) was several minutes in

length, with occasional mind (and body) numbing pauses of up to 10 min between capture events.

An examination of the data of Sebens and Koehl (1984) shows that even under the best conditions, the interval between capture events must be over a minute for *Alcyonium* and 2 min for *Metridium*. Barange and Gili (1988) sampled the coelenteron contents of a benthic hydroid over a diel cycle. From their data [mean prey items captured *per* (polyp · day), number of polyps *per* colony], I calculated the average interval between capture events to be about 1.3 min. Thus, passive suspension feeding for these organisms is a *slow* process for non-patch concentrations of prey. Cnidarian colonies snag particles slowly from the water when a patch isn't around, unlike some vertebrate suspension feeders that capture enormous quantities of particles in the same period of time (Sanderson and Wassersug, 1990).

Saturation of colonies remains a puzzling phenomenon

The utility of this model is that it points out some new directions for work with passive suspension feeding cnidarians. An unanswered question is why are these filters not adapted for high efficiency filtration under high particle fluxes? Is there a biological constraint on the system that limits feeding? Constraints found in other suspension feeding systems include saturation of the filter (Parker, 1975; Real, 1977) or gut-filling (Doyle, 1979). Neither of these constraints appears likely for this species. *Alcyonium* colonies began slowing their feeding rate long before most polyps had successfully fed once. They are also capable of packing many prey items into a single polyp (Patterson, 1984). Lasker *et al.* (1982) showed that in single-polyped *Hydra*, the ingestion of prey was controlled by previous feeding events, *i.e.*, prey captured later in a feeding bout were less likely to be ingested than prey caught near the beginning. Burnett *et al.* (1960) and Hand (1961) showed that nematocyst discharge in *Hydra* is inhibited by food in the gastrovascular cavity, and Lasker *et al.* (1982) speculate that this may be important in limiting ingestion rate. But Ruch and Cook (1984) have demonstrated inactivation of nematocyst discharge even in the absence of food in the gut. This startling observation was explored further by Clark and Cook (1986) using a colonial hydroid. They provide evidence from lab feeding experiments that the accumulation of discharge products from the stenotele nematocysts used by this hydroid in prey capture is sufficient to inhibit further feeding, and that it is not necessary to invoke waste product accumulation from digestion, or depletion of nematocysts, to explain the phenomenon. For those cnidarians exhibiting this interesting feedback, the second assumption of the model (see Introduction) could easily be reformulated to incorporate a term specifying the diffusion time of the nematocyst discharge

products. It is unknown whether nematocyst discharge products affect *Alcyonium* in a similar fashion.

The nerve net is also probably involved in the process of modulating prey capture in cnidarians (McFarlane, 1978). Deformation of the tentacle by repeated particle impactions may be important in producing inhibition of nematocyst discharge during feeding in plankton patches. On a larger scale, flow induced deformation of the entire colony may be important in regulating the rate process of prey capture. Best (1988) found that feeding rate in a sea pen, *Ptilosarcus*, increased then decreased with flow speed and attributed this behavior to changes in volume flow rate that occurred as the filtering surfaces changed their orientation. A similar phenomenon was noted in a crinoid (Leonard *et al.*, 1988).

Some experiments that would help solve the mystery of why colonies saturate long before all filtering units (polyps) have fed would include (1) stealing particles from the tentacles after capture but before transfer to the mouth, while monitoring frequency of capture and attempted ingestion events, (2) eliciting repeated nematocyst discharge by micromolar diffusion clouds of amino acids from a micropipette near tentacle tips or mechanical stimulation of tentacles while the cnidarian colony is simultaneously feeding, (3) separating a cnidarian colony into two halves except for a strip of tissue and examining feeding rates in the two halves before and after the connection is severed [Clark and Cook (1986) found no effect for a hydroid], and (4) offering digestible and non-digestible prey to a species that will ingest both types of particles (*cf.* Lasker *et al.*, 1983) and measuring feeding rates on both types of particles separately and together while nematocyst discharge products are monitored.

It is very intriguing that this colonial octocoral saturates after a few minutes of feeding in high prey densities at about the same number of prey that would be caught over a 2–4 h period in the field (Sebens and Koehl, 1984). Digestion of prey items renders them unidentifiable after 4–6 h (Sebens and Koehl, 1984). Have these colonial suspension feeders evolved to “charge their capacitance” on a time scale of approximately two hours because they are limited by the activity of their digestive enzymes? For boreal cnidarians in the Atlantic, the strongest tidal flows will be obtained for a 2–4 h period between slack tides. Because plankton patches are the exception rather than the rule, the feeding response may have evolved to cope with sparse prey moving past the colony over a 2–4 h period. During periods of flow dominated by wave-driven oscillations, *e.g.*, slack tides, colonies will re-filter water already low in prey. Feeding in a bi-directional flow can actually increase feeding success in a hydroid exposed to high (patch) concentration of prey (Hunter, 1989). At present, it is unknown for this species whether feeding

effectiveness is higher in bi-directional flow at low prey concentrations.

Application of this model to other passive suspension feeders will test its generality and provide evidence for whether the dichotomy in feeding behavior characteristic of this species when feeding in low and high prey concentrations is a widespread phenomenon. Future developments in the measurement and description of plankton patchiness on a small scale in nearshore waters (Pieper and Holliday, 1985) and description of the benthic boundary layer in which these organisms live (Jumars and Nowell, 1984) will improve our ability to model and understand this fascinating process.

Acknowledgments

Discussions with P. Basser, B. Best, R. Etter, T. Givnish, R. Grosberg, S. Kleinhaus, W. McFarland, T. McMahon, R. Olson, S. L. Sanderson, K. Sebens, R. Turner, the HUMP seminar group, and the Aquatic Sciences group at M. I. T., have improved the paper greatly. P. Rudy, Acting Director, Marine Science Center, Northeastern University, Nahant, Massachusetts, kindly provided laboratory space. C. Alexander and B. Otteson provided technical assistance. Financial support for this project was provided by the Richmond Fund of Harvard University, the Lerner-Gray Fund for Marine Research of the American Museum of Natural History, NSF OCE-8308958 to K. Sebens of Harvard University, a Faculty Research Award from UC Davis, and NSF OCE-8716427 to the author.

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